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THE RELATIONSHIPS OF THE EUPHORBIEAE (EUPHORBIACEAE)¹

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ABSTRACT

The Euphorbieae and Hippomaneae, though both usually placed in subfamily Euphorbioideae, differ in many inflorescence details and can be linked unambiguously only by one cryptic character: the rod-shaped starch grains in the latex. While the Hippomaneae have inflorescences very similar to those of many other members of the Euphorbiaceae, the Euphorbieae have an inflorescence so specialized that one seems to be forced to relate it to other members of the family through a hypothetical ancestor with a synflorescence of axillary bisexual cymes more primitive than most extant taxa possibly other than *Jatropha*.

A primary aim of this symposium is to review critically Webster's (1994) classification of the Euphorbiaceae. This paper is an attempt to share a speculation arising from misgivings over the supposed homogeneity of the subfamily Euphorbioideae. This is not a presentation of the results of prolonged and detailed research but rather speculations arising while producing a routine Flora account of the Euphorbiaceae for the *Flora of Ethiopia* (31 genera, 209 species), coupled with a long-standing interest in *Euphorbia* (the largest genus within the Ethiopian flora), particularly the succulent species. A Flora writer should delve into the larger scale taxonomy of those families that must be covered, but is rarely allowed the time to carry out anything more than superficial investigations on taxa not actually included in the Flora. Thus the following ideas must not be regarded as anything more than simple-minded speculations.

Determining the relationships of a group as specialized as the Euphorbieae used to be of little concern to a Flora writer. The matter became a little more relevant with the advent of cladistics, where the methodology demands a working hypothesis of probable sister groups and character polarization. Sooner or later such methods should be applied to the Euphorbiaceae in general, and ideally to the Euphorbieae in particular, where there are inconsistencies in current generic delimitation. How, for instance, would a cladistic analysis relate *Chamaesyce*, very widely recognized as a distinct genus, to the various sections within *Euphorbia* subg. *Agaloma* and the rest of *Euphorbia*? There are many other interesting problems waiting to be tackled: What is the relationship

between the Old World and New World species of *Euphorbia*? How do the subgenera *Euphorbia* and *Lacanthia* (sensu Gilbert, 1987) relate to the rest of the genus? Such an analysis, in my view, could do much to clarify these relationships and thus the taxonomy of the tribe as a whole. It would demand a much greater knowledge of the possible origins of the Euphorbieae than is available. In a group so morphologically isolated, speculation is needed.

The Euphorbieae and Hippomaneae are included within the subfamily Euphorbioideae along with three other tribes (Stomatocalyceae, Pachystromateae, and Hureae) that have usually been associated with the Hippomaneae (Webster, 1994), primarily on the basis of their caustic milky latex from nonarticulate laticifers, frequently glandular bracts, and often highly reduced flowers that always lack petals. This juxtapositioning has not always been the case: Mueller Argoviensis (1866) and Bentham (1878) placed these groups at opposite ends in their sequences. There are indeed major differences in inflorescence morphology between the two groups such that I felt forced to consider the possibility that the similarities were the product of convergence. One unusual cryptic character, very characteristic, rod-shaped starch grains found in the latex, is a good contender for a synapomorphy, which suggests that they do have a common origin. This in turn led to an attempt to reconstruct a possible ancestral inflorescence type from which the modern plants could have evolved most parsimoniously.

The rod-shaped starch grains have not been reported in other members of the Euphorbiaceae, although many taxa appear never to have been

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surveyed (Rudall, 1987), and their discovery elsewhere in the family would be a serious challenge to the taxonomic integrity of the Euphorbioideae. The toxicity of the latex has also been mentioned as a linking character but the major compounds involved—diterpene esters—occur also in subfamily Crotonoideae (Beutler et al., 1989). The pollen of the Euphorbioideae is rather uniform (Punt, 1987), but the pollen type is apparently plesiomorphic; thus the similarity should be treated with caution. Morphological evidence is even less clear-cut. There are superficial similarities in that most taxa in both groups have a sparse to nonexistent indumentum of simple hairs but there are many exceptions in both major tribes, such as species of *Chamaesyce* and *Agaloma* within *Euphorbia* and members of the Mabeinae and many species of *Stillingia* within the Hippomaneae, and such evidence can only be regarded as essentially negative: it does not disprove the possibility of a relationship. The tendency toward very reduced flowers, rare in the family as a whole, has also been invoked to support a common grouping. It is possible, theoretically, to select a reduction series for the flowers within the Hippomaneae from genera such as *Mabea*, which have well-defined perianths and male flowers with many stamens, through to *Dalembertia*, in which the male flower is reduced to a single sepal and a single stamen and the female flower has only vestigial remnants of the perianth. This sequence could be regarded as continued by the Euphorbieae, where the male flower is always reduced to a single naked anther and the female flower to a naked ovary. There is evidence of a female perianth in many genera within the Euphorbieae, including some species of *Euphorbia*, but the only clear indication of a male perianth, beyond an articulation between pedicel and filament, is the vestigial male perianth seen in *Anthostema* and *Dichostemma*. There has been a temptation to suggest that this sequence gives a true guide to relationships, but this must be questioned—could the Hippomaneae really have given rise directly to the Euphorbieae?

The major difference between the two groups is the inflorescence structure, which is discussed at length below. Details of floral morphology, most notably the very different styles, also suggest that the Euphorbieae and Hippomaneae may not be closely related. In the Euphorbieae the styles are relatively short, usually divided, and have more or less capitate stigmas. Studies indicate that most species are pollinated by a variety of often unspecialized insects, the exception being a group of New World taxa, most obviously the genus *Pedi-*

lanthus but also various red-flowered *Euphorbia* species, pollinated by birds. In most members of the Hippomaneae the styles are undivided, long and tapered, and are usually characteristically circinately coiled when young. There are not many observations of pollination. The pendent inflorescences and long stigmas of some species suggest that wind pollination is a possibility, but other genera have well-developed nectaries within the inflorescences indicating some form of animal pollination, perhaps most often by small unspecialized insects (Bawa et al., 1985), but in at least one case, *Mabea occidentalis* Benth. (Steiner, 1983), predominantly by bats. Thus the significance of the striking differences in the styles is not clear. Another possibly significant difference is the frequency of succulence within the Euphorbieae where it has clearly evolved several times independently, whereas succulence appears to be almost absent in the Hippomaneae, recorded only from a few Brazilian species of *Stillingia* (Rogers, 1951).

The contrast in inflorescence organization between the Hippomaneae and the Euphorbieae seems so great that one must consider whether the similarities between them could be the result of convergence rather than an indication of common ancestry. If the most reasonable (parsimonious) hypothetical common ancestor has to have characters such that it would have to be placed within one of the other subfamilies, notably the Crotonoideae, rather than the Euphorbioideae, the Euphorbioideae would have to be regarded as a grade rather than a clade.

There seems to be little or no case for questioning the homogeneity of the tribe Euphorbieae as it is clearly defined by the very peculiar inflorescence—the cyathium—distinct from all other inflorescence types seen within the family. Linnaeus and other very early authors, plus one of the two giants of nineteenth-century Euphorbiaceae taxonomy, Baillon (1874), thought that the cyathium was a hermaphroditic flower. However, the alternative theory that it was an inflorescence was mentioned by Lamarck as early as 1788 and is now unquestioned, though there is still disagreement in the exact interpretation of its organization. The cyathium consists of a cupular receptacle with marginal lobes usually regularly alternating with glands, sometimes quite complex in structure, enclosing a whorl of groups of male flowers inserted below each lobe, plus their associated bracteoles, and a single, central female flower, often reduced to a naked ovary. There is quite a lot of variation within this theme with regard to features such as the number of parts within the involucre and the

amount of fusion between them and the occasional presence of a small perianth on the male and female flowers, but no genera can be regarded as having inflorescences truly intermediate between a cyathium and any other inflorescence recorded within the family. There has been much debate on the nature of the cyathium but the weight of evidence (e.g., Schoute, 1937) seems to support the scheme suggested by Eichler (1878), in which each involucre lobe/bract subtends a monochasium of male flowers.

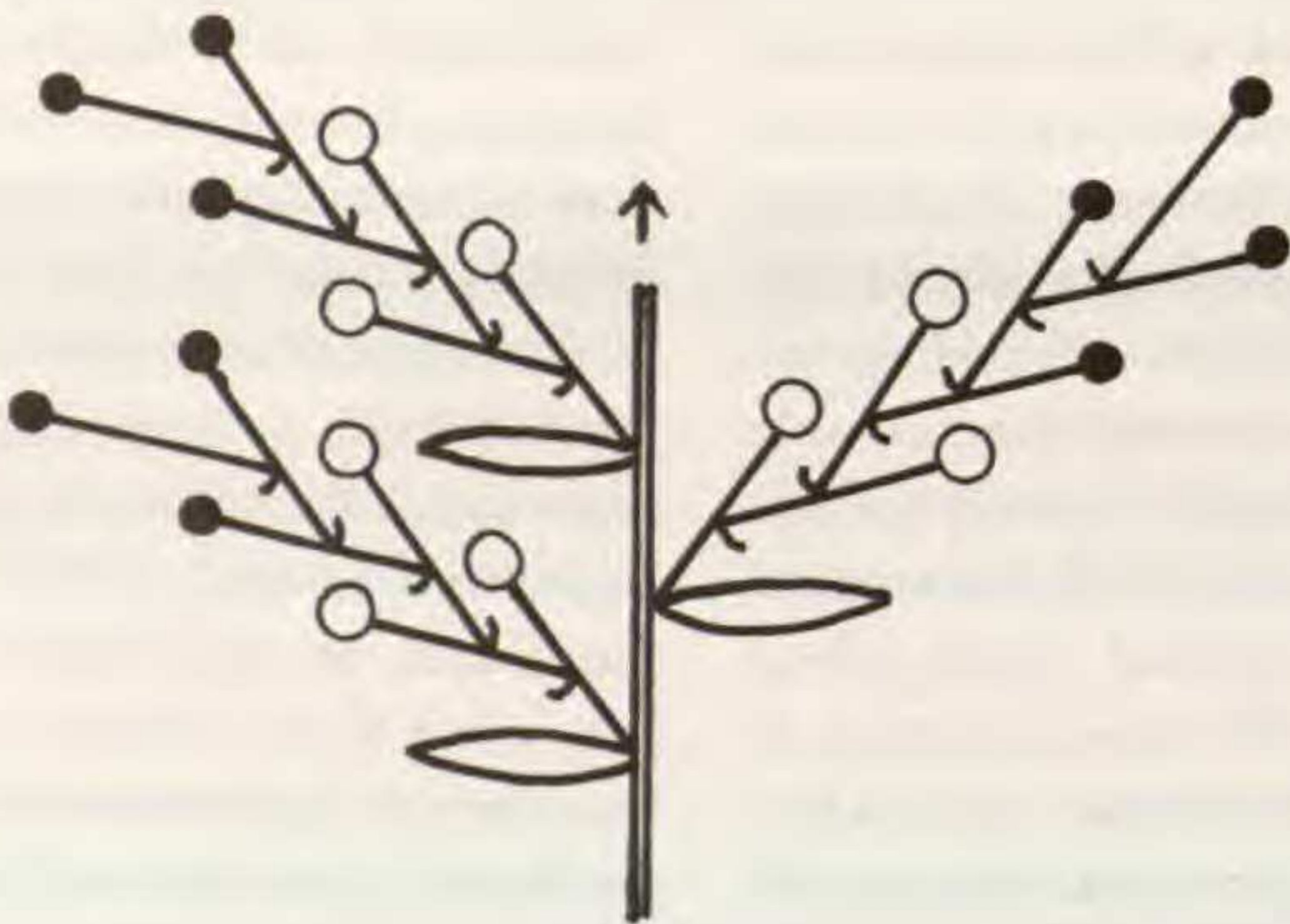
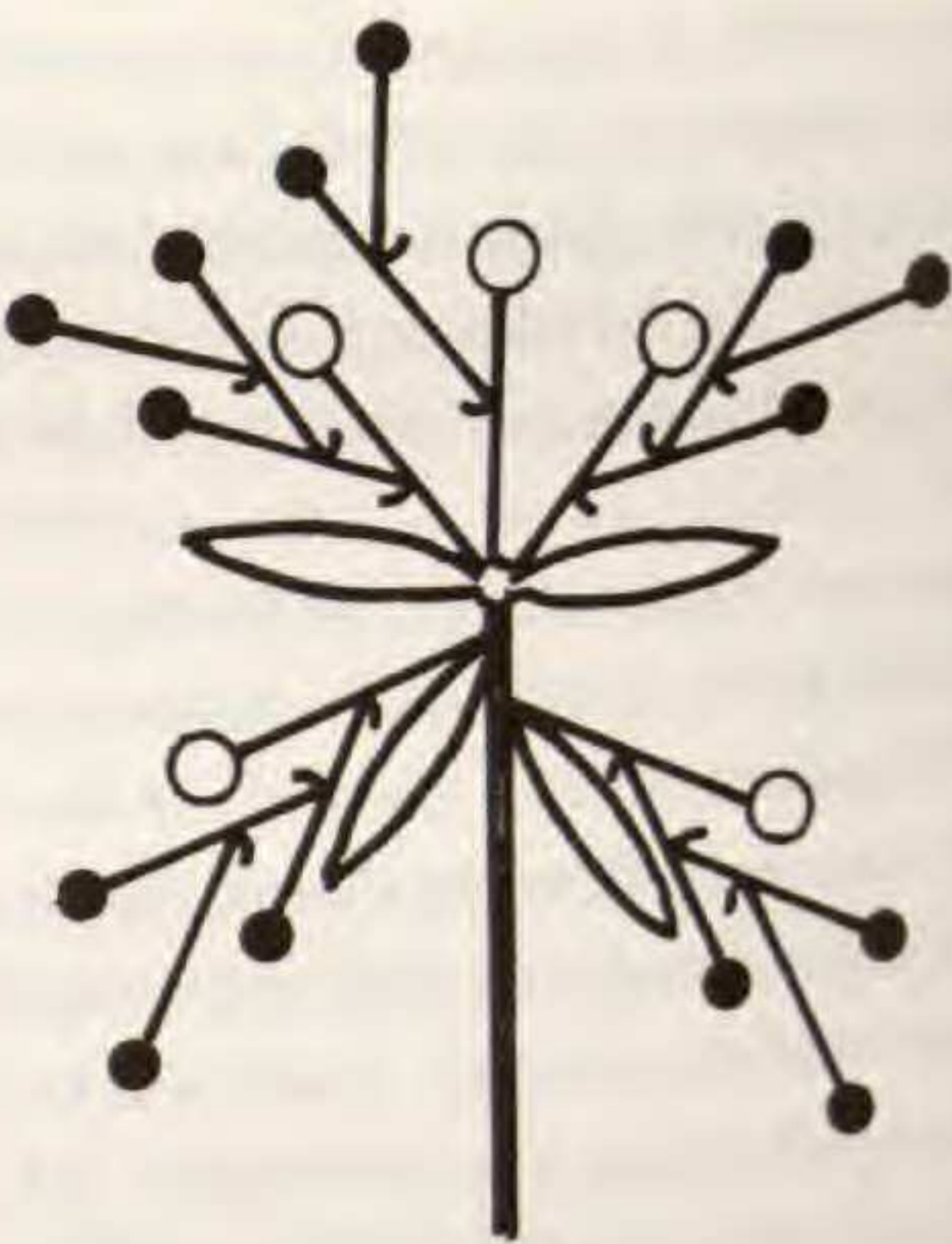
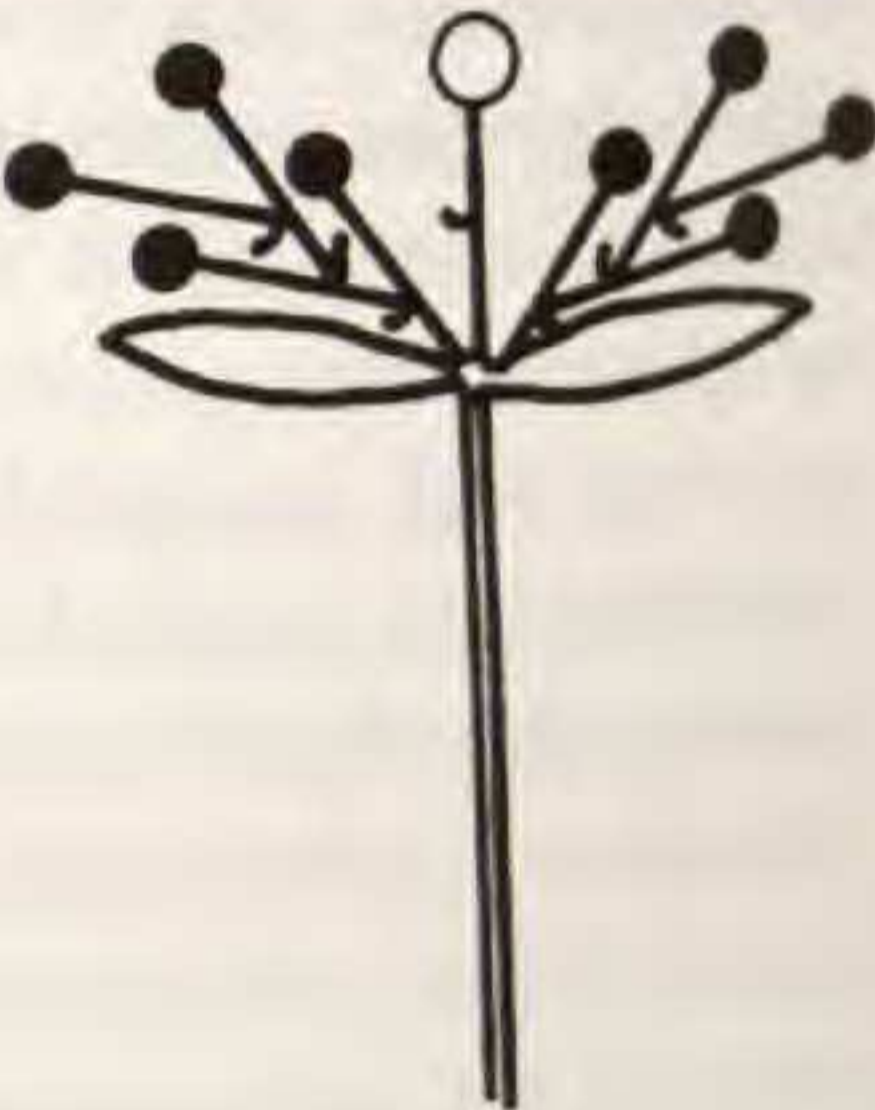
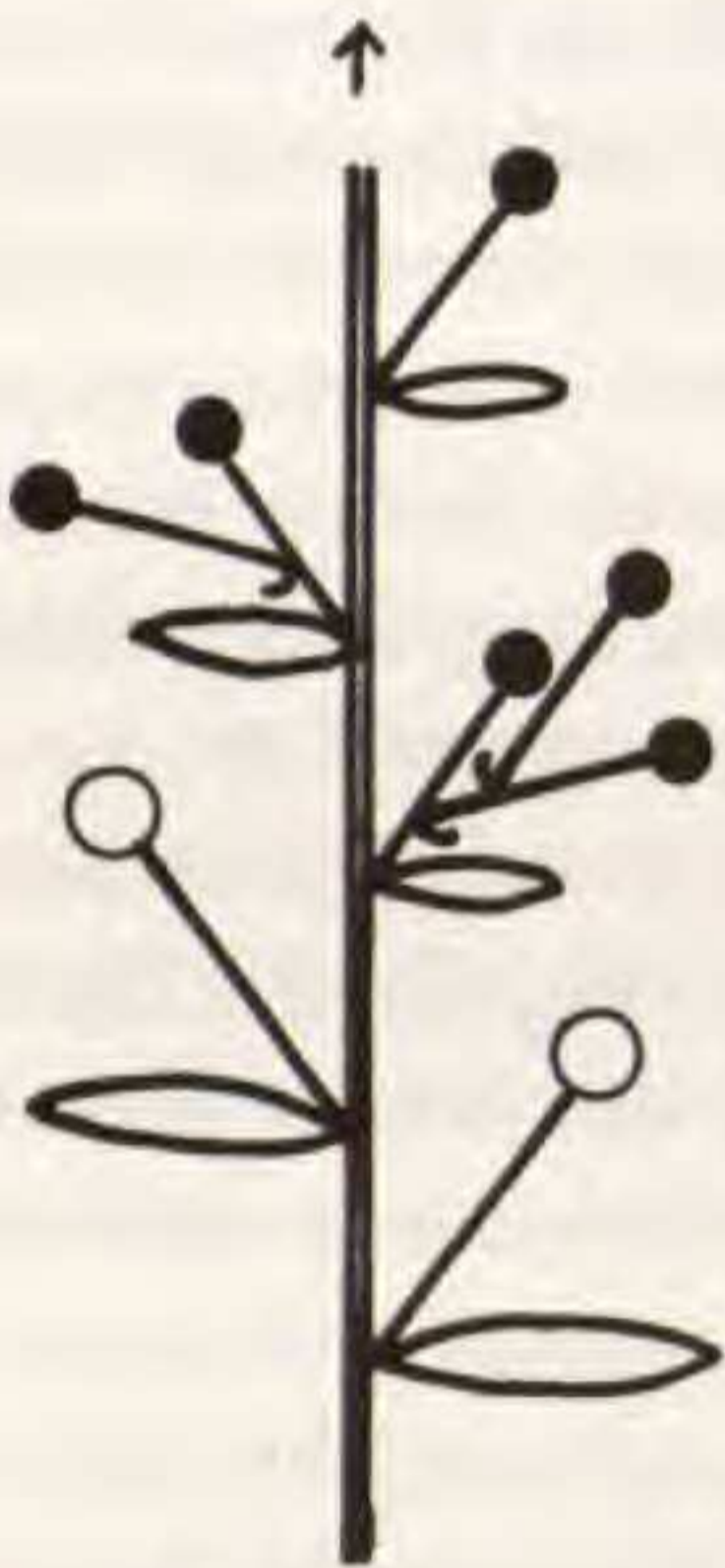
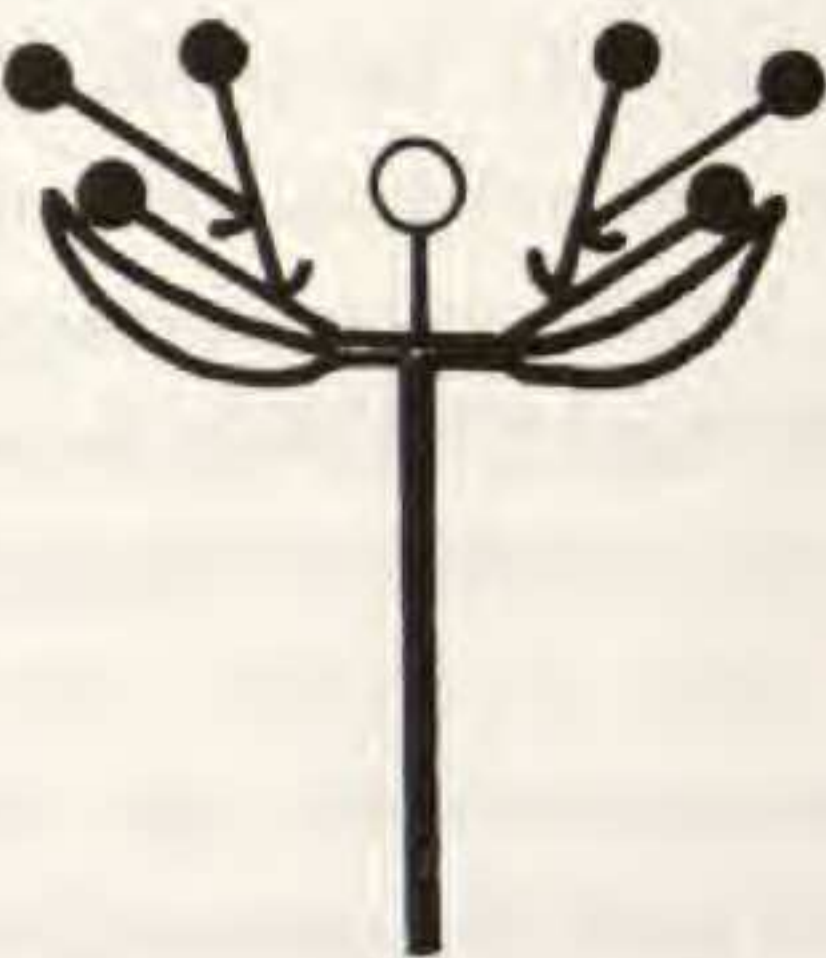
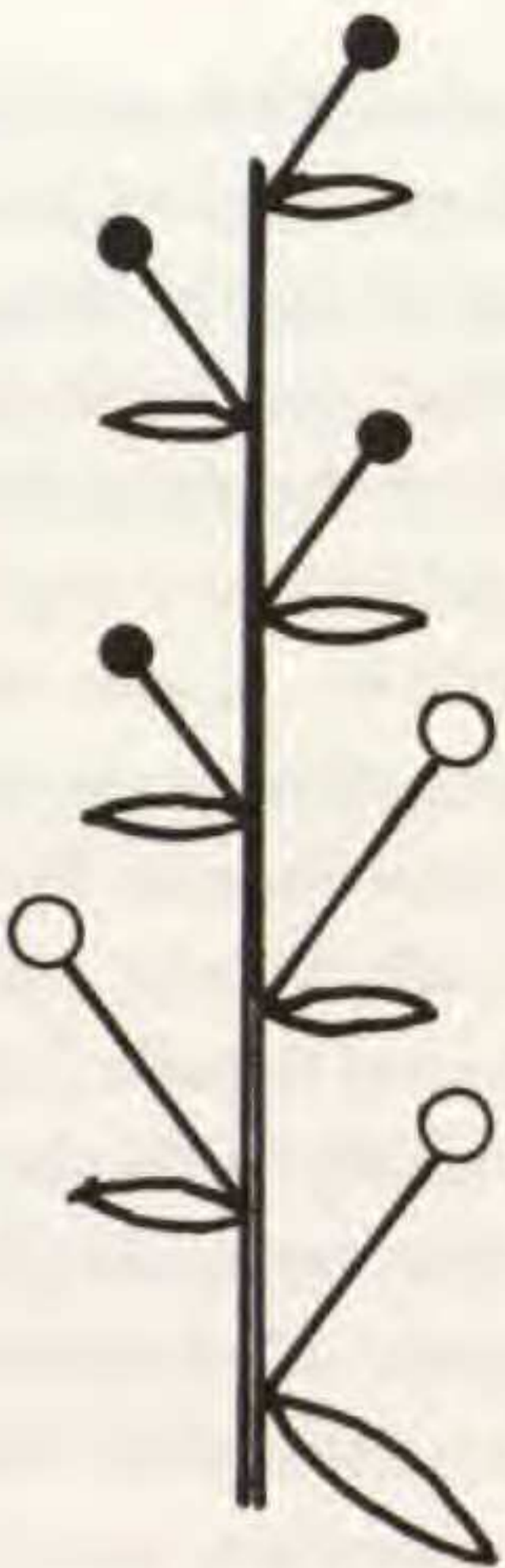
The cyathium contrasts very strongly in organization with the inflorescences of the vast majority of other members of the family, including the other tribes placed within subfamily Euphorbioideae by Webster. There is a fundamental division within the Euphorbiaceae between the uniovulate tribes, with only one ovule per ovary locule, and the biovulate tribes, with two ovules per locule. The biovulate tribes are distinct in so many features of anatomy and morphology that they will not be considered in detail. It might, however, be worth making the observation that the axillary fascicles of flowers characteristic of the vast majority of biovulate taxa must be considered rather specialized reduced inflorescences. Most other uniovulate tribes, including the Hippomaneae, have inflorescences that are generally regarded as cymose, but many show an essentially racemelike organization in which the cymose nature of the ultimate elements is only betrayed by the fact that some of the male flowers are in very reduced cymules rather than solitary as in a true raceme. The contrast with the Euphorbieae is further increased by the fact that, as in the vast majority of the genera of the Euphorbiaceae, the female flowers are proximal and the male flowers distal. Such an arrangement within an elongated inflorescence has a structural logic: female flowers produce bulky, longer-lived fruits requiring the transport of nutrients; male flowers are usually smaller, short-lived, and only require a transient supply of nutrients. It would be functionally illogical to have to maintain an extra length of stem at the base of an inflorescence once the male flowers had finished, especially as the extra length would mean that the stem would have to be that much stronger mechanically. By having distal male flowers, that part of the stem does not need to transport as many nutrients for so long, does not need to be strong enough to support relatively heavy fruits, and can be shut down as soon as the male flowers have dispersed their pollen. Having said this, there is an obvious exception to such logic—*Acalypha*—which shows a bewildering array of inflorescence types, particularly with

regard to the relative positions of male and female flowers, and must be regarded as a special case.

To convert a typical Hippomaneae inflorescence into a cyathium one must postulate a considerable condensation of the main inflorescence axis, a relatively straightforward and common evolutionary process. However, at the same time one must also postulate a complete reversal in the relative position of the male and female flowers or the loss of the proximal female flowers plus the *de novo* production of a terminal female flower. The latter process seems particularly difficult to account for unless one invokes the terminal allomorphic flowers seen in some species of *Acalypha*. There would also have to be a reversal of the general trend of the reduction of the distal male inflorescences. An alternative scheme would be to derive the cyathium from a group of thyrses. Such a scenario is very similar to that proposed below and must be given consideration. The one fact against it is the cymose arrangement of the groups of male flowers within the cyathium. It is difficult to imagine a racemelike inflorescence giving rise to such a grouping.

A more parsimonious scenario is to postulate that both the Hippomaneae and the Euphorbieae evolved from a common ancestor which had a thyse—a synflorescence in which an indefinite fertile axis produced a spiral series of axillary bisexual cymes (Fig. 1). The cymes could be either dichasial or monochasial or, perhaps quite likely, initially dichasial with monochasial ultimate branches such as is frequently seen with *Jatropha*. The Hippomaneae inflorescence could (and surely did) evolve by a simple process of reduction with the proximal cymes being reduced to single female flowers and the distal cymes reduced to cymules of male flowers or eventually to single male flowers. The Euphorbieae would have to be derived by a more complex evolutionary process centered primarily on a great condensation of the main synflorescence axis to produce a dense head of cymes, the central one, perhaps in response to the protected situation, becoming reduced to a single female flower while the surrounding whorl of cymes became all male and their associated subtending bracts and ?stipular glands fused to form an involucre.

An alternative scenario is that the cyathium has evolved from a single cyme with a primary female flower and lateral male flowers such as is seen in *Jatropha*. Croizat (1938), in discussing *Neoguilauminea*, accepted such a scenario and expressed the belief that 4-lobed involucres were the basic type for the Euphorbieae, derived presumably from the initial two levels of branching of a dichasium.



An immediate difficulty is the frequency of 5-lobed involucre, which would be difficult to derive from a regular dichasial cyme but which could be expected as the norm if the involucre was the product of the condensation of a Fibonacci spiral derived from a thyrs. Two further bits of evidence argue against a development from a single cyme. First is the situation in *Neoguillauminea*, where the central female flower appears to be subtended by four separate involucre of male flowers, which indicates that several inflorescences are involved. Second, some species in *Euphorbia* sect. *Esula* (notably *E. cyparissioides* Pax) have groups of male flowers and glands very similar to those of the involucre intermingled within the involucre proper in a possible spiral series. Such a situation could be explained easily if the axis of the cyathium was a contracted synflorescence, but is very much more difficult to explain if the structure was derived from a single cyme.

Unmodified simple cymes are of rather rare occurrence within the family and among African taxa are only found in *Jatropha*, a genus showing a number of other apparently primitive features, most notably the well-developed corolla and female flowers with staminodes occasionally so well developed (e.g., in *J. tropaeolifolia* Pax) that the flowers appear to be bisexual. Another unusual character of *Jatropha* is the diversity of laticifer types, a feature that has been interpreted as an indication of primitiveness (Dehgan & Craig, 1978; Rudall, 1987). The cymes of most species of *Jatropha* are primarily dichasial, but in many species (*J. spicata* Pax is a good example) the ultimate branches are usually long monochasia of male flowers. This suggests that there is a natural tendency within the organization of such cymes for reduced terminal elements to be monochasial, which would support Eichler's (1878) interpretation of the cyathium.

Dehgan & Craig (1978) discussed the possibility of a *Jatropha*-like plant being ancestral to the Crotonoideae. It seems a distinct possibility that any common ancestor of the Hippomaneae and the Euphorbieae might also have had *Jatropha*-like cymes, thus opening up the question of subfamily relationships. The cymes of most *Jatropha* species

are strictly terminal and show no tendency toward the production of a synflorescence. Perhaps the strictly terminal position of the inflorescence in such *Jatropha* is a factor in their having retained their clearly cymose organization while other groups with axillary cymes have evolved the thyrs (and cyathia?) now so widespread in the family. However, the most primitive species (Dehgan & Schutzman, 1994, this issue), *J. curcas* L., does produce a synflorescence such as is postulated here as the common ancestral form for cyathia and for the thyrses of most other uniovulate Euphorbiaceae. This would seem to reinforce the view that *Jatropha* might represent the nearest approach to an ancestral type for the family as a whole.

In conclusion, it is suggested that it is not possible for the cyathium to have evolved from any inflorescence found within modern-day Hippomaneae (and closely allied tribes). One must conjecture a rather primitive common ancestor belonging to neither group but rather to the Crotonoideae. If this is indeed the case, it might be better to extend the Euphorbioideae to include the Crotonoideae, as suggested in effect by Mahlberg et al. (1987). Alternatively, if an independent relationship of each group to a very primitive member of the family be accepted, there might be a good case for placing the Hippomaneae and allies in a subfamily of their own and restricting the Euphorbioideae to the Euphorbieae.

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FIGURE 1. Diagrammatic representation of the hypothetical evolution of, on the left, the racemelike inflorescences of the Hippomaneae (and most other Crotonoideae and Acalyphoideae) and, on the right, the cyathium from a hypothetical synflorescence of axillary bisexual cymes. For simplicity the cymes are shown as monochasia, but in practice are more likely to be primarily dichasial. On the left there is a progressive elongation of the main axis and a reduction of the axillary cymes. On the right there is a shortening of the main axis to form a dense cluster of cymes, a central, terminal cyme becoming reduced to a single female flower and surrounded by a whorl of all-male cymes, while the associated subtending leaves and stipules fuse to form an enclosing involucre.